**Exploring the Relationship between Paleobiogeography, Deep-Diving Behavior, and Size Variation of the Parietal Eye in Mosasaurs**

**By**

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Submitted to the graduate degree program in Geology and the Graduate Faculty of the University of Kansas in partial fulfillment of the requirements for the degree of Master of Arts.

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## ABSTRACT

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The parietal eye (PE) in modern squamates (Reptilia) plays a major role in regulating body temperature, maintaining circadian rhythms, and orientation via the solar axis. This study is the first to determine the role, if any, of the PE in an extinct group of lizards. We analyzed variation in relative size of the parietal foramen (PF) of five mosasaur genera to explore the relationship between PF size and paleolatitudinal distribution. We also surveyed the same specimens for the presence of avascular necrosis—a result of deep-diving behavior—in the vertebrae. *Plioplatecarpus* had the largest PF followed by *Platecarpus*, *Tylosaurus*, *Mosasaurus,* and *Clidastes*. A weak relationship exists between paleolatitudinal distribution and PF size among genera, as *Plioplatecarpus* had the highest paleolatitudinal distribution (~78°N) and the largest PF among genera. *Clidastes*, *Mosasaurus, Platecarpus*, and *Tylosaurus*, however, shared a similar northern paleolatitude (~55°N) extent despite *Platecarpus* having a statistically larger PF than the other three genera ($p<0.001$ in Fisher's LSD test). *Mosasaurus, Plioplatecarpus*, and *Tylosaurus* also shared a similar southern paleolatitude (~64°S) despite *Plioplatecarpus* having a larger PF. There is no correlation between PF size and paleolatitudinal distribution for specimens within genera. We found no relationship between PF size and presence of avascular necrosis. *Tylosaurus* and *Mosasaurus,* which exhibited avascular necrosis, had a similar PF size to *Clidastes,* which did not avascular necrosis. The PE of mosasaurs may have functioned primarily for navigation and orientation related to migration; however, this possibility requires further study of modern PE-bearing organisms and its function.

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# CHAPTER 1. EXPLORING THE RELATIONSHIP BETWEEN PALEOBIOGEOGRAPHY, DEEP-DIVING BEHAVIOR, AND SIZE VARIATION OF THE PARIETAL EYE IN MOSASAURS

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Parietal Foramen, *Plioplatecarpus*, *Platecarpus*, Avascular Necrosis, *Mosasaurus*

## ABSTRACT

The parietal eye (PE) in modern squamates (Reptilia) plays a major role in regulating body temperature, maintaining circadian rhythms, and orientation via the solar axis. This study is the first to determine the role, if any, of the PE in an extinct group of lizards. We analyzed variation in relative size of the parietal foramen (PF) of five mosasaur genera to explore the relationship between PF size and paleolatitudinal distribution. We also surveyed the same specimens for the presence of avascular necrosis—a result of deep-diving behavior—in the vertebrae. *Plioplatecarpus* had the largest PF followed by *Platecarpus*, *Tylosaurus*, *Mosasaurus,* and *Clidastes*. A weak relationship exists between paleolatitudinal distribution and PF size among genera, as *Plioplatecarpus* had the highest paleolatitudinal distribution (~78°N) and the largest PF among genera. *Clidastes*, *Mosasaurus, Platecarpus*, and *Tylosaurus*, however, shared a similar northern paleolatitude

(~55°N) extent despite *Platecarpus* having a statistically larger PF than the other three genera ($p<0.001$ in Fisher's LSD test). *Mosasaurus, Plioplatecarpus*, and *Tylosaurus* also shared a similar southern paleolatitude (~64°S) despite *Plioplatecarpus* having a larger PF. There is no correlation between PF size and paleolatitudinal distribution for specimens within genera. We found no relationship between PF size and presence of avascular necrosis. *Tylosaurus* and *Mosasaurus,* which exhibited avascular necrosis, had a similar PF size to *Clidastes,* which did not avascular necrosis. The PE of mosasaurs may have functioned primarily for navigation and orientation related to migration; however, this possibility requires further study of modern PE-bearing organisms and its function.

## INTRODUCTION

The importance of the parietal eye (PE), also known as the pineal eye, in mosasaurs has yet to be determined as no studies have examined its function in this ancient group of marine reptiles. Additionally, no studies have examined the function of the PE in any extinct group of animals so this study is the first to determine if ancient animals used their PE similarly to their modern counterparts. Today, the PE is found only in some frogs, lampreys, Lepidosauria (squamates plus *Sphenodon*), salamanders, and toads (Tosini, 1997). The PE is located on the dorsal, posterior part of the skull and can be between the two frontal bones, the two parietal bones (PB), or in the frontoparietal suture (Fig. 1). The PE possesses a cornea, retina, and lens; however, the PE can only sense the presence of light (Edinger, 1955). The parietal foramen (PF) is the orifice in the skull that holds the PE, which is connected to the pineal gland. Collectively, the PE, PF, and pineal body comprise the pineal complex.

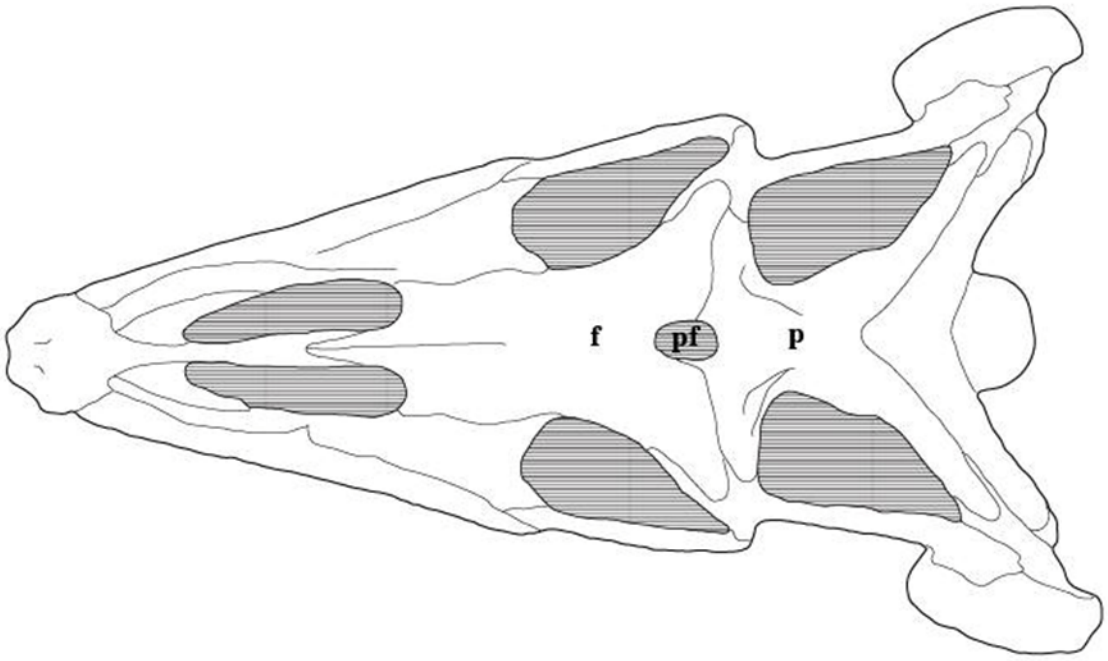



**Figure 1**. Dorsal view image of a *Plioplatecarpus* skull. Frontal bone (**f**), parietal foramen (**pf**) and parietal bone (**p**) are labeled. Image courtesy of Oceans of Kansas website at http://oceansofkansas.com/kansplio.html.

The primary function of the pineal complex is maintaining circadian rhythms, body temperature, and orientation via the solar axis (Ralph, 1975). In particular, the pineal complex generally becomes more pronounced and larger for animals living in high (and generally cooler) latitudes, possibly as a result of selection for increased sensitivity to lower intensity sunlight (Ralph, 1975; Quay 1980). For example, Davenport et al. (2014) proposed that the pineal body triggers migration in the leatherback sea turtle, *Dermochelys coriacea*, due to seasonal variation in day length. This turtle has a thin PB—referred to as a skylight by Davenport et al. (2014)—which allows greater absorption of the low intensity sunlight at higher latitudes by the pineal body. *Dermochelys* also migrates seasonally to high latitudes, such as Newfoundland (~49°N) (Goff et al., 1988), Scotland (~55°N)

(Davenport et al., 2014), and northern Norway (~71°N) (Carriol and Vader, 2002) before they return to their Caribbean nesting grounds. Davenport et al. (2014) noted that no other group of migratory sea turtles possesses a similarly modified PB, nor do they migrate to as high of latitude as *D. coriacea*. Gundy et al. (1975), likewise, found that most agamid (Squamata: Agamidae) and iguanid (Squamata: Iguanidae) lizards lacking a PE are restricted to ≤ 10° of the equator, whereas PE-bearing lizards of the same genera are found up to 55° from the equator. Gundy et al. (1975) concluded that PE-bearing lizards are better adapted to the more extreme daily and seasonal temperature variations of higher latitudes than those that do not have a PE. A biogeographical study of lizard skulls in the University of Kansas Herpetology Collection found similar results, as such temperate-latitude lizards as *Holbrookia maculata* (Squamata: Phrynosomatidae) have a larger PF—a proxy for the PE—than such equatorial lizards as *Stenocercus variabilis* (Squamata: Tropiduridae) (Appendix 1). Labra et al. (2010), however, found no relationship between latitudinal or altitudinal distribution or local environmental temperatures to PE size in 30 species of the South American lizard *Liolaemus* (Squamata: Liolaemidae). These contradictory results complicate our current understanding of the function of the PE in lizards in terms of thermoregulation and circadian rhythms.

Lizards also use their PE to orient themselves relative to their environment (e.g., Gundy et al., 1975, Freake, 2001, Beltrami et al., 2010). Beltrami et al. (2010) demonstrated that the ruin lizard, *Podarcis sicula* (Squamata: Lacertidae), orients spatially via an internal compass and reference to solar cues. When the PE of test subjects was experimentally ablated, orientation performance declined. Freake (2001) displaced individuals of the Australian sleepy lizard, *Tiliqua rugosa* (Squamata: Scincidae), 800 m

84 from their home range, and found that only individuals with a functional PE returned to
85 their home range. This nonmigratory species would also occasionally leave their home
86 range for reproduction, employing olfaction and visual cues (presumably including solar
87 cue detection via the PE). Similarly, Ellis-Quinn and Simon (2004) found that specimens of
88 Yarrow's spiny lizard, *Sceloporus jarrovi*, had a significantly higher percentage of
89 individuals returning to their natural home range (after being displaced 150 m away) with
90 an uncovered PE compared to those with a covered PE. Although many experiments have
91 been conducted to understand the function of the PE in extant lizards, no studies have
92 explored the function of the PE—using the PF as its proxy— in ancient squamates.
93 We studied the relative size of the PE in five mosasaur genera to determine whether
94 the PE in an extinct group of lizards functioned similarly to that of their extant relatives.
95 Mosasaurs (Squamata: Mosasauridae), a group of marine lizards that lived during the Late
96 Cretaceous Period, may have used their PE to help regulate their circadian rhythms,
97 maintain body temperature, or orient themselves relative to sea-penetrated sunlight.
98 Mosasaurs are an excellent group of ancient organisms to determine the function of their
99 PE. There is an obvious difference in the relative size of their PF (Fig. 2) and they have a
100 global distribution (e.g., Russell, 1967, Kear et al., 2005, Páramo-Fonseca, 2011, Fernández
101 and Gasparini, 2012, Leblanc et al., 2012), both of which could help resolve if PE size and
102 paleolatitudinal distribution correlate. What is more difficult to determine is if mosasaurs
103 used their PE for orientation as we cannot study their behavior directly relative to the rays
104 of the sun. We can analyze, however, their bone structures to determine what diving
105 behavior each mosasaur genera had. Some mosasaur genera (e.g., *Platecarpus*,
106 *Plioplatecarpus*, *Tylosaurus*) were probably deep-diving predators based on the presence of

avascular necrosis—bone tissue that has very porous spongy structure produced by degassing within the bone while ascending from deep to shallow water (i.e., the bends)—in the vertebrae (Rothschild and Martin, 2005). Perhaps these deep-diving mosasaurs had a large, light-sensitive PE which could orient them in their low-light environment. Shallow-dwelling mosasaurs, likewise, would not need a pronounced PE due to the high amount of light stimuli in their environment.

**Figure 2**. Dorsal view of mosasaur parietal bones in **A**, *Mosasaurus* (RBINS VF AR 42-12); **B**, *Platecarpus* (SMU 76351); **C**, *Plioplatecarpus* (RMM 7071); and **D**, *Tylosaurus* (RMM 5610). Scale bar equals 5 cm.

As such, we propose two hypotheses (H1, H2; Table 1) to explain the function of the PE in mosasaurs: H1) PF size increases as paleolatitudinal distribution of fossil specimens increases; and H2) PF size is relative to the amount of avascular necrosis in mosasaur vertebrae. For H1 and H2, the PF length is used as a proxy for PE size. For H1, we compare the PF size to paleolatitudinal distribution among and within mosasaur genera. Hypothesis 1 is falsified if there is no relationship between PF size and paleolatitudinal distribution. For H2, a larger PF is associated with a greater number of vertebrae affected by avascular necrosis. Hypothesis 2 is falsified if there is no relationship between PF size and amount of avascular necrosis in the mosasaur vertebrae.

| Hypotheses | Description |
|---|---|
| H1 | Size of parietal foramen increases for mosasaurs in higher paleolatitudes, both within and among genera |
| H2 | Size of parietal foramen is larger in mosasaurs evidence of avascular necrosis compared to mosasaurs without it. |

**Table 1.** Descriptions for Hypothesis One (H1) and Hypothesis Two (H2).

**Institutional Abbreviations—ALMNH PV**, the Alabama Museum of Natural History, Tuscaloosa, Alabama, U.S.A.; **FHSU**, the Fort Hays Sternberg Museum, Hays, Kansas, U.S.A.; **FMNH**, the Field Museum of Natural History, Chicago, Illinois, U.S.A.; **ING**, Servicio Geológico Colombiano, Bogota, Columbia; **KHM**, Kaikoura Historical Museum, Kaikoura, New Zealand; **KUVP**, the University of Kansas Museum of Natural History, Lawrence, Kansas, U.S.A.; **M**, Canadian Fossil Discovery Centre (previously

Morden and District Museum), Morden, Manitoba, Canada; **MLP**, Museo de La Plata, Buenos Aires, Argentina, **MNHN**, the Muséum National D'histoire Naturelle, Paris, France; **NMC**, Canadian Museum of Nature, Ottawa, Ontario; **NMNZ**, the National Museum of New Zealand, Wellington, New Zealand; **OCP**, Office Chérifien des Phosphates, Khouribga, Morocco; **RBINS**, the Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; **RMM**, the Mcwane Center, Birmingham, Alabama, U.S.A.; **SMU**, the Shuler Museum of Paleontology at the Southern Methodist University, Dallas, Texas, U.S.A; **TMP**, the Royal Tyrell Museum of Paleontology, Drumheller, Alberta, Canada; **UALVP**, University of Alberta Laboratory for Vertebrate Paleontology, Calgary, Alberta, Canada; **UNO**, University of New Orleans, New Orleans, Louisiana, U.S.A.; **USNM**, National Museum of Natural History, Washington D.C., U.S.A.; **WDC**, Wyoming Dinosaur Center, Thermopolis, Wyoming, U.S.A.; **YPM**, Yale Peabody Museum, New Haven, Connecticut, U.S.A.

## MATERIALS AND METHODS

### Material

We examined five mosasaur genera: *Clidastes* (n=13); *Mosasaurus* (n=5); *Platecarpus* (n=13); *Plioplatecarpus* (n=10); and *Tylosaurus* (n=10). We chose these taxa because of their: (1) variation in PF size (see Fig. 2); (2) paleolatitudinal distribution (Fig. 3); and (3) abundance in various fossil collections in North America and in Europe (Table 2). We took special effort to measure nonKansan mosasaurs to ensure a diverse paleolatitudinal range among the five genera, as Kansan mosasaurs are found in museums worldwide. We only included data from mosasaurs with a well-preserved PB. We measured

158 other mosasaur genera, such as *Prognathodon* and *Tethysaurus* (see Table 2), but their

159 sample size was too small to be included in these analyses.


160

161 **Figure 3**. General location of all mosasaur specimens measured in the northern hemisphere.

162 1) *Mosasaurus*; 2) *Platecarpus*; 3) *Clidastes*, *Mosasaurus*, *Platecarpus*; 4) *Clidastes*,

163 *Plioplatecarpus*, *Tylosaurus*; 5) *Platecarpus*, *Tylosaurus*; 6) *Clidastes*, *Plioplatecarpus*,

164 *Tylosaurus*; 7) *Mosasaurus*, *Plioplatecarpus*.

165

| Catalogue # | Species Name | Location | Length of Parietal Foramen (PF) (mm) | Length of Parietal Bone (PB) (mm) | PF/PB |
|---|---|---|---|---|---|
| YPM 1333 | *Clidastes liodontus* | Kansas: Graham County, Solomon River | 2.3 | 50.5 | 0.046 |
| ALMNH PV 2005.0006.0006 | *Clidastes liodontus "moorevillensis"* | Alabama: Greene County | 4.6 | 72.5 | 0.063 |
| YPM 1368 | *Clidastes propython* | Kansas: Wallace County, 23 miles east of Fort Wallace | 3.3 | 42.7 | 0.077 |

| | | | | | |
|---|---|---|---|---|---|
| FSHU 17576 | *Clidastes propython* | Kansas: Logan County, Coal Oil Canyon | 4.75 | 48.03 | 0.099 |
| FMNH P 27324 | *Clidastes propython* | Alabama: Dallas County, 3 miles southeast of Harrell Station | 7.949 | 113.71 | 0.070 |
| FMNH PR 495 | *Clidastes propython* | Kansas: Logan County | 7.838 | 89.841 | 0.087 |
| ALMNH PV 1985.0012.0001 | *Clidastes propython* | Alabama: Greene County | 3.4 | 59.6 | 0.057 |
| RMM 2423 | *Clidastes propython* | Alabama: Greene County | 4 | 57.5 | 0.070 |
| TMP 1983.019.002 | *Clidastes propython* | South Dakota: Pennington County | 7.8 | 109.3 | 0.071 |
| ALMNH PV 1998.0001.0001 | *Clidastes sp.* | Alabama: Greene County | 3.9 | 47.3 | 0.082 |
| ALMNH PV 2002.0002.0001 | *Clidastes sp.* | Alabama: Greene County | 2.6 | 45 | 0.058 |
| USNM-PAL 537823 | *Clidastes sp.* | Kansas | 2.9 | 60.8 | 0.048 |
| MNHN PMC 14 | *Halisaurus arambourgi* | Morroco: Near Grand Daoui area | 12.935 | 69.507 | 0.186 |
| WDC CPM-100 | *Halisaurus arambourqi* | Morroco | 11.9 | 57.4 | 0.207 |
| USNM 442450 | *Halisaurus platyspondylus* | Maryland: Prince Georges County, Oxon Hill | 10.1 | 55.802 | 0.181 |
| SMU PA 18 | *Halisaurus sp.* | Angola: Bentiaba | 11.6 | 74.3 | 0.156 |
| FMNH PR 467 | *Latoplatecarpus nichollsae* | South Dakota: Custer County | 29 | 166.8 | 0.174 |
| TMP 1984.162.0001 | *Latoplatecarpus willistoni* | Manitoba: Morden | 14.4 | 93.1 | 0.155 |
| KUVP 1034 | *Mosasaurus horridus* | South Dakota: Custer County | 10.695 | 160.75 | 0.067 |
| RBINS VF AR 42/12 | *Mosasaurus lemmonnieri* | Belgium: Hainaut Province, Ciply | 8.98 | 79.65 | 0.113 |

| | | | | | |
|---|---|---|---|---|---|
| RBINS VF AR 42/15 | *Mosasaurus lemmonnieri* | Belgium: Hainaut Province, Spiennes | 9.612 | 108.569 | 0.089 |
| RBINS VF AR 42/8 | *Mosasaurus lemmonnieri* | Belgium: Hainaut Province, Ciply, | 9.333 | 85.711 | 0.109 |
| TMP 2003.400.01 | *Mosasaurus sp.* | Alberta: South of Lethbridge | 18.837 | 214.584 | 0.088 |
| YPM 1112 | *Platecarpus ictericus* | Kansas: Logan County, Russell Springs | 13.2 | 70 | 0.189 |
| YPM 3690 | *Platecarpus ictericus* | Kansas: Gove or Lane County | 10.2 | 62.8 | 0.162 |
| M.74.02.02 | *Platecarpus sp.* | Manitoba: Pembina Escarpment | 24.7 | 122.2 | 0.202 |
| YPM 24907 | *Platecarpus sp.* | Kansas: Wallace County | 17.3 | 83.4 | 0.207 |
| USNM 412454 | *Platecarpus sp.* | Kansas: Logan County near Scott City | 13.4 | 89.1 | 0.150 |
| M.74.09.03 | *Platecarpus tympaniticus* | Manitoba: Pembina Escarpment | 14.2 | 92.2 | 0.154 |
| M.73.08.02 | *Platecarpus tympaniticus* | Manitoba: Pembina Escarpment | 16.3 | 92.4 | 0.176 |
| KUVP 1085 | *Platecarpus tympaniticus* | Kansas: Logan County, Hell Creek | 8.2 | 47.8 | 0.172 |
| SMU 76351 | *Platecarpus willistoni* | North Central Texas | 13.8 | 72.8 | 0.190 |
| FHSU 17314 | *Plesioplatecarpus planifrons* | Kansas: Gove County, Tuffle Ranch | 11.7 | 74.7 | 0.157 |
| RBINS 3100 | *Plioplatecarpus houzeaui* | Belgium: Hainaut Province, Ciply | 35.5 | 72.687 | 0.488 |
| RBINS 3101 | *Plioplatecarpus houzeaui* | Belgium: Hainaut Province, Ciply | 26.1 | 66.45 | 0.393 |
| RBINS 3108 | *Plioplatecarpus houzeaui* | Belgium: Hainaut Province, Ciply | 30 | 54.05 | 0.555 |
| RBINS R 36 | *Plioplatecarpus houzeaui* | Belgium: Hainaut Province, Ciply | 28.512 | 63.67 | 0.448 |

| | | | | | |
|---|---|---|---|---|---|
| RBINS R 40 | *Plioplatecarpus houzeaui* | Belgium: Limburg Province, Kanne | 26.592 | 74.654 | 0.356 |
| NMC 11840 | *Plioplatecarpus primaevus* | South Central Saskatchewan | 30.48 | 71.19 | 0.428 |
| NMC 11835 | *Plioplatecarpus primaevus* | South Central Saskatchewan | 28.2 | 66.41 | 0.425 |
| KU UNO 8611-2 | *Plioplatecarpus sp.* | Alabama: Coatopa County | 49.129 | 112.431 | 0.437 |
| RMM 7071 | *Plioplatecarpus sp.* | Kansas: Unknown, in Mooreville Chalk, possibly Greene County | 27.6 | 78 | 0.354 |
| SMU PA 149 | *Prognathodon kianda* | Angola: Bentiaba | 9.2 | 110.2 | 0.083 |
| RBINS R33 | *Prognathodon solvayi* | Belgium: Mons Basin | 18.666 | 96.109 | 0.194 |
| SMU 70356 | *Russellosaurus coheni* | Texas: Dallas County: Cedar Hills | 2.18 | 54.899 | 0.040 |
| FHSU 13910 | *Selmasaurus johnsoni* | Kansas: Gove County | 5.248 | 93.4 | 0.056 |
| MNHN 1999-9 GOU2 | *Tethysaurus nopcsai* | Morocco: Goumima region | 5.882 | 59.549 | 0.099 |
| USNM PAL 537824 | *Tylosaurus dyspelor* | Kansas | 17.594 | 212.948 | 0.083 |
| FHSU 15632 | *Tylosaurus kansensis* | Kansas: Gove County | 5.6 | 56.73 | 0.099 |
| FHSU 2209 | *Tylosaurus nepaeloicus* | Kansas: Rooks County | 8.5 | 183.03 | 0.046 |
| KB-MC-M-16/SMU 76546 | *Tylosaurus nepaeolicus* | Texas: Brewster County, 10 km southwest of Terlingua Ghost Town | 13.5 | 135.1 | 0.100 |
| Triebold "Sophie" | *Tylosaurus proriger* | Texas: Ellis County | 18.5 | 286.9 | 0.064 |
| ALMNH PV 1993.0001.0001 | *Tylosaurus proriger* | Alabama: Greene County | 9.9 | 155 | 0.064 |
| RMM 5610 | *Tylosaurus proriger* | Alabama: Hale County | 8.4 | 92.3 | 0.091 |

| | | | | | |
|---|---|---|---|---|---|
| TMP 1982.050.0010 | *Tylosaurus proriger* | Kansas: Graham County | 10.3 | 142.2 | 0.072 |
| YPM 3990 | *Tylosaurus proriger* | Kansas: Wallace County | 10.2 | 130.57 | 0.078 |
| YPM 3993 | *Tylosaurus proriger* | Kansas: Wallace County | 7.6 | 146.18 | 0.052 |

**Table 2.** Measurements recorded for the parietal foramen (PF) length, the parietal bone (PB) length, and the PF/PB for every specimen along with its excavated locality. Note that some locality data are incomplete, such as USNM PAL 537824, and were not used for testing H2 within genera.

## Methods

Each skull was photographed using a Sony Cyber-shot DSC-H90 16.1 MP Digital Camera. We analyzed each photograph with J. Microvision v1.27 to obtain exact measurements of the PB and PF length (see Fig. 1), and calculated the relative size of the PF by comparing the length of the PF to the length of the PB (i.e., PF/PB). We needed to measure the relative size of the PF as large mosasaurs, like *Tylosaurus* (see Fig. 2), would naturally have a larger PF compared to smaller mosasaurs like *Clidastes.* As such, the PB was used as it gave us a high amount of measured individuals and ensured that PF size would not be skewed towards mosasaur body size, We then calculated the average PF size for each genera using Minitab® version 17 (Fig. 4). We also determined the paleolatitudinal coordinates for each specimen from the Paleobiology Database Website (paleobiodb.org), with the highest known distribution for all genera presented in Table 3.

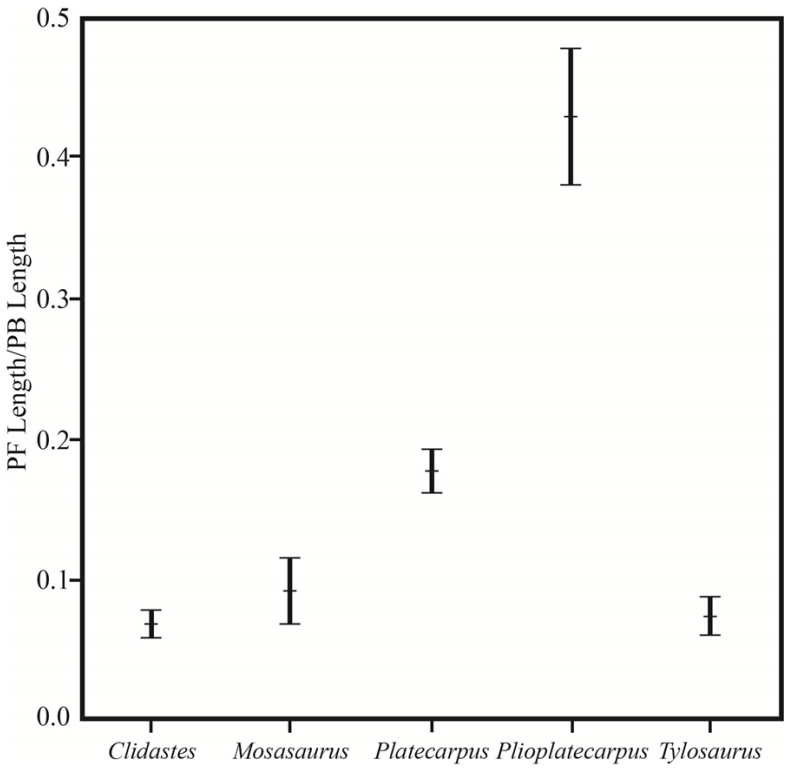
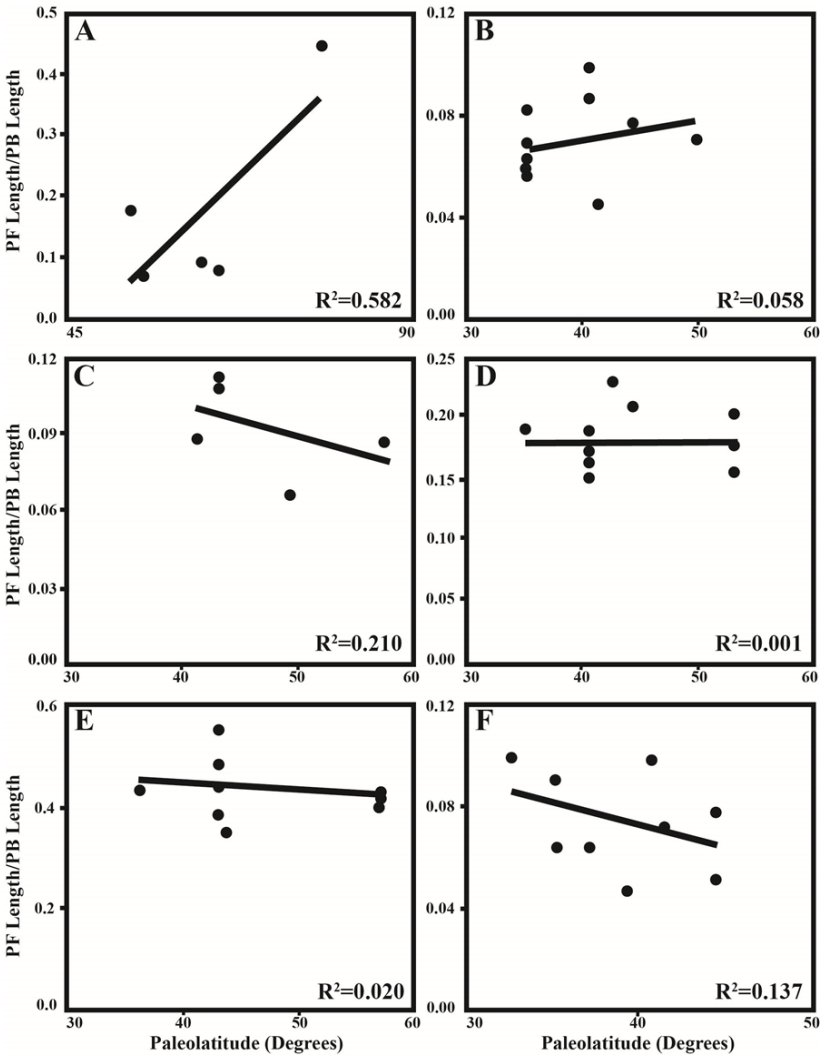



**Figure 4.** Average PF size among genera with standard deviation bars. A LSD test indicated there was significant differences between *Clidastes*, *Mosasaurus*, and *Tylosaurus* to *Platecarpus* ($p<0.001$) and there was a significant difference between *Platecarpus* to *Plioplatecarpus* ($p<0.001$).

| Mosasaur Genera | Highest Southern Paleolatitude Distribution | Highest Northern Paleolatitude Distribution |
|---|---|---|
| *Clidastes* | N/A | 54.7°N (Sternberg, 1915) |
| *Mosasaurus* | 62.6°S (Fernández and Gasparini 2012) | 57.1°N (Nicholls and Russell, 1990) |
| *Platecarpus* | 17°S (Bengtson and Lindgren, 2005) | 53.7°N (Bardack, 1968) |
| *Plioplatecarpus* | 62.6°S (Fernández and Gasparini 2012) | 78.2°N (pers comm. T. Konishi) |
| *Tylosaurus* | 64.6°S (Warren and Speden, 1978) | 53.7°N (Bardack, 1968) |

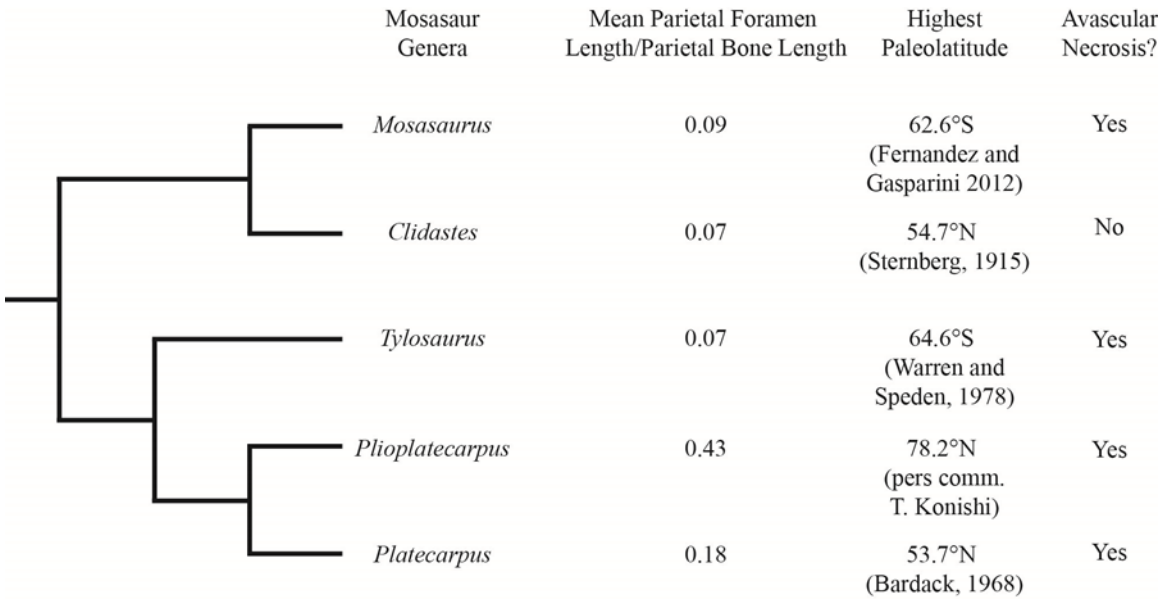
191 **Table 3.** Highest known northern and southern paleolatitudinal distribution for *Clidastes*,
192 *Mosasaurus*, *Platecarpus*, *Plioplatecarpus*, and *Tylosaurus*. Note *Clidastes* is restricted to
193 the Northern Hemisphere.
194
195 We performed both a nonphylogeny and a phylogeny analysis for H1. A phylogeny
196 analysis was performed to determine if there was an evolutionary relationship between PF
197 size among genera and paleolatitudinal distribution. For the nonphylogeny analysis,
198 Minitab® version 17 was used to perform a One-Way Analysis of Variance (ANOVA) and
199 a follow up *post hocs* (Fisher's Least Significant Difference [LSD] test) to determine if the
200 genera were significantly different (alpha=0.05) (Fig. 4). A linear regression model was
201 then used to determine the relationship between PF size and paleolatitude for both among
202 and within genera (H1; Fig. 5) (alpha=0.05). For the phylogeny analysis, R version 3.2.2
203 (Fire Safety) (R Code Team) was used to perform a phylogenetic independent contrasts
204 (PIC) (Felsenstein, 1985) analysis, while assuming a Brownian motion process, using a
205 modified version of the mosasaur phylogenetic tree provided by Bell (1997) (alpha=0.05)
206 (Fig. 6). R converted both the PF/PB ratio and paleolatitudinal distribution to their
207 independent contrasts—by way of R library ape (Paradis et al., 2004) and caper (Orme et
208 al., 2013) using the "crunch" function—and then calculated their correlation through the
209 origin (Fig. 7). For H2, an ANOVA was used to test for PF size differences between taxa
210 that lack avascular necrosis (i.e., *Clidastes*) versus genera that possess this character (i.e.,
211 *Mosasaurus*, *Platecarpus*, *Plioplatecarpus*, and *Tylosaurus* (Table 4).




212

213 **Figure 5**. Relationship between paleolatitudinal distribution and parietal foramen (PF)
214 length over parietal bone length (PB) (PF/PB) among genera. All paleolatitudinal points
215 were acquired from the Paleobiology Database Website (paleobiodb.org). **A**, graphical
216 representation of the most extreme paleolatitudinal distribution for each mosasaur genera.
217 The sources for each extreme paleolatitudinal point can be found on Table 3. **B**, *Clidastes*;
218 **C**, *Mosasaurus*; **D**, *Platecarpus*; **E**, *Plioplatecarpus*; **F**, *Tylosaurus* are graphical
219 representations of the relationship between paleolatitude and PF/PB for specimens within
220 genera. Only specimens with known fossil locality information were used.

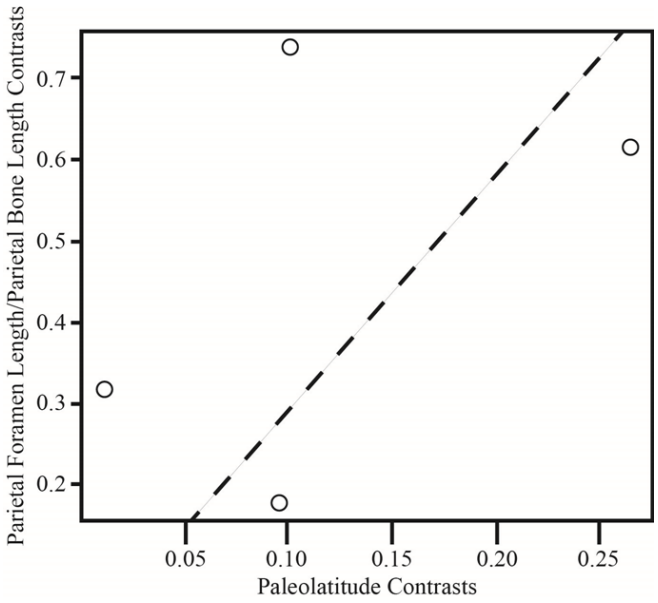
221




222

223 **Figure 6.** A generalized mosasaur tree displaying the five main genera studied for the
224 experiment along with their mean parietal foramen length/parietal bone length (PF/PB)
225 ratio, highest paleolatitude known, and presence of avascular necrosis. Tree modified from
226 Bell (1997) and avascular necrosis data came from Rothschild and Martin (2005). Branch
227 lengths were set to be equal.

228




229

**Figure 7**. Plot of the residual independent contrasts of parietal foramen length/parietal bone length against the residual independent contrasts of paleolatitude among the five mosasaur genera ($R^2$=0.601, p=0.077). The line of regression intercepts at (0,0).

| Mosasaur Genera | Presence of avascular necrosis |
|---|---|
| *Clidastes* | no |
| *Mosasaurus* | yes |
| *Platecarpus* | yes |
| *Plioplatecarpus* | yes |
| *Tylosaurus* | yes |

**Table 4.** Presence or absence of avascular necrosis in mosasaurs from Rothschild and Martin (2005).

## RESULTS

*Plioplatecarpus* had the largest PF with an average PF/PB ratio of 0.43 (SD=0.06), followed by *Platecarpus* (PF/PB=0.18, SD=0.02), *Mosasaurus* (PF/PB=0.09, SD=0.02), *Tylosaurus* (PF/PB=0.07, SD=0.02), and *Clidastes* (PF/PB=0.07, SD=0.02) (Fig. 4). The ANOVA found statistically significant differences in PF size among genera (F=201.28, DFn=4, DFd=40, p<0.001). A follow up Fisher's LSD test determined three significantly different groups among the five genera: Group A (*Plioplatecarpus*), Group B (*Platecarpus*), and Group C (*Clidastes*, *Mosasaurus*, and *Tylosaurus*) (p<0.001).

For H1, the nonphylogeny-oriented, linear regression model determined that there was a weak but nonsignificant correlation between PF size and paleolatitude when all genera were considered ($R^2$=0.582, p=0.134) (Fig. 5A). The phylogeny-oriented PIC analysis falsified the hypothesis, as there was a weak but nonsignificant correlation

($R^2$=0.601, p=0.077) (Fig. 7) between contrasts in PF size and contrasts in paleolatitudinal distribution. Within genera, a linear regression model determined that *Clidastes* and *Plioplatecarpus* had a positive but negligible correlation between PF size and paleolatitude ($R^2$ <0.1), whereas *Mosasaurus, Platecarpus*, and *Tylosaurus* exhibited weak and negative correlations between PF size and paleolatitude ($R^2$ <0.25) (Fig. 5B–F).

An ANOVA falsified H2 as *Mosasaurus* and *Tylosaurus,* which displayed avascular necrosis symptoms, have a PF size similar to that of *Clidastes* (see above LSD test), which did not possess avascular necrosis (Table 4; Rothschild and Martin, 2005). *Plioplatecarpus* and *Platecarpus* also had significantly larger PF size than both *Mosasaurus* and *Tylosaurus* even though these four genera all displayed symptoms of avascular necrosis.

## DISCUSSION

### Paleolatitudinal Distribution among Genera

Both the nonphylogeny and PIC analyses falsified H1 as there is a weak but nonsignificant relationship between PF size and paleolatitudinal distribution. In the linear analysis, the correlation coefficient and p-value ($R^2$=0.582, p=0.134) indicates a weak and nonsignificant correlation between PF size and paleolatitude. Furthermore, the PIC analysis indicates that the evolution of a large PF does not associate with the evolution of more extreme latitudinal distribution in mosasaurs ($R^2$=0.601, p=0.077) (Fig. 7). *Plioplatecarpus* had by far the largest PF, as determined by a Fisher's LSD test, and the highest paleolatitudinal distribution (~78°N) (T. Konishi, personal communication, 2013) of the five genera studied. A large PF suggests that *Plioplatecarpus* had a large PE, which would likely have been more sensitive to low-intensity sunlight compared to such smaller PF-

bearing mosasaurs as *Tylosaurus*. Although *Plioplatecarpus* had the most northern distribution and the largest PF, it shared nearly equal southern paleolatitudinal extremes (~64°S) with such smaller PF-bearing mosasaurs as *Mosasaurus* and *Tylosaurus* (Fernández and Gasparini, 2012). *Clidastes*, *Mosasaurus, Platecarpus*, and *Tylosaurus* also had a similar northern paleolatitudinal distribution (~55°N) even though *Platecarpus* had a larger PF than *Clidastes, Mosasaurus,* and *Tylosaurus* ($p<0.001$ in Fisher's LSD test) (Sternberg, 1915; Bardack, 1968, Nicholls and Russell, 1990) (see Fig. 3–4, Table 3).

If, in the future, additional specimens of *Platecarpus* are discovered at or described from latitudes > 55°, correlation between PF size and paleolatitudinal distribution may be stronger and can push both the linear regression analysis ($p=0.134$) and the PIC analysis ($p=0.077$) p-values to significant values. There are already several partial remains of mosasaurs found in Australia that are tentatively described as *Platecarpus* (Kear et al., 2005). These specimens have a slightly higher paleolatitudinal range (~58°S) than the current specimens found in southern Canada (Bardack, 1986). *Platecarpus* specimens are also likely to be found at the Anderson River site in the Northwest Territories of Canada (see Russell, 1967) and could further extend their paleolatitudinal range to ~78°N. Given that *Platecarpus* are more abundantly found in the northern part of the Western Interior Seaway (Nicholls and Russell, 1990), finding a *Platecarpus* specimen at the Anderson River site would not be unlikely. If this were to happen, an additional PIC analysis could give us a significant p-value and reveal a correlation between the evolution of PF size and latitudinal distribution.

**Paleolatitudinal Distribution within Genera**

296 Hypothesis 1 within genera was falsified, as there is no apparent relationship
297 between PF size and paleolatitudinal distribution for the specimens analyzed. There was a
298 very weak to negligible correlation among the five genera ranging from $R^2$=0.210 to 0.001
299 (Fig 5B–E). The PF size for each individual showed almost no association with its fossil
300 locality. The weak correlation between PF size and paleolatitude indicates the absence of an
301 association between PE and local latitudinal position.
302 Alternatively, the lack of a relationship between PF size and paleolatitudinal
303 distribution within mosasaur genera may, instead, reflect an adaptive value of the PE (i.e.,
304 PF by proxy) with a role related to the onset of migration behavior. Mosasaurs with a larger
305 PE size may have a behavioral response to day length (sensed with the PE) and initiate
306 migration across different latitudes, following the intensity of solar radiation. These
307 movements may have taken such mosasaurs as *Plioplatecarpus* from northern Canada (e.g.,
308 Anderson River site in the Northwest Territories during the Late Cretaceous; ~78°N) to
309 southern Alabama (e.g., Mobile area during the Late Cretaceous; ~30°N). This would allow
310 the mosasaurs to maintain their circadian rhythm and body temperature as incident sunlight
311 angle increased at lower latitude during shorter daylight hours experienced during the
312 (present day) winter months. This explanation is based on homing and migrational
313 behaviors exhibited by extant reptiles that are controlled by the pineal complex (e.g.,
314 Freake, 2001; Ellis-Quinn and Simon, 2004) and the study of the migrational effects of the
315 pineal body on *Dermochelys coriacea* (Davenport et al., 2014). The thinning of the PB in
316 *D. coriacea* is analogous to the PE in extant and extinct squamates, as both structures
317 would allow a greater amount of sunlight to be absorbed by the pineal body. If the rather
318 large and highly exposed pineal body in *D. coriacea* triggers migration via the relative

amount of day length, then, perhaps, mosasaurs with a large PE, like *Plioplatecarpus,* used their PE and pineal body for migration in the Western Interior Seaway during the Late Cretaceous.

**Presence of Avascular Necrosis vs. PF size among Genera**

Hypothesis 2 is falsified, as there is no relationship between PF size and presence of avascular necrosis. If there was a relationship, we would have seen mosasaurs with a small PF (*Clidastes*, *Mosasaurus*, and *Tylosaurus*) not display characteristics of avascular necrosis while the opposite would hold true for mosasaurs with a large PF (*Platecarpus* and *Plioplatecarpus*). This was not the case as specimens of *Clidastes* did not exhibit avascular necrosis, whereas *Mosasaurus*, *Platecarpus*, *Plioplatecarpus*, and *Tylosaurus* did. Thus, there is no correlation between these two features in mosasaurs. Interestingly, Rothschild and Martin (2005) reported that *Plioplatecarpus* had a smaller percentage range of vertebrae affected by avascular necrosis (5–17%), whereas *Platecarpus* had a much greater percentage range of affected vertebrae (10–64%). Their study is consistent with our rejection of H2, as *Plioplatecarpus* has the significantly largest PF and would have a greater range of vertebrae affected by avascular necrosis when compared to *Platecarpus*.

**Resolving the Function of the PF**

Although H1 explains *Plioplatecarpus* and its significantly large PF, the purpose of the large PE in *Platecarpus* versus other mosasaurs ($p<0.001$ in Fisher's LSD test) is still unclear (see Figs. 2, 4). Neither H1 nor H2 explains the size difference versus paleolatitude or presence of avascular necrosis.

342 To resolve the function of the PE in *Platecarpus* and other mosasaurs, we encourage
343 further fieldwork to discover mosasaur-bearing strata as they may lead to new discoveries
344 of previously unidentified mosasaurs, fill in the paleobiogeographical gaps in the fossil
345 record (e.g., Northwest Territories in Canada, Australia, Antarctica), and produce more
346 specimens with intact PB. Although there is a particular interest in the paleobiogeographic
347 range of the five genera analyzed here, other mosasaur genera measured for this study are
348 also of interest, such as *Prognathodon* and *Tethysaurus.* Additional genera will be
349 beneficial in performing a follow-up PIC analysis, as this may provide a stronger, more
350 robust understanding of the evolutionary relationship between PF size and latitudinal
351 distribution of mosasaurs. The greatest challenge in determining the true
352 paleobiogeographical range of mosasaurs is the extreme high-latitude field sites, as they are
353 located in either inhospitable or highly isolated locations. Mosasaurs from these sites would
354 provide insight into whether the PF was different in size or shape for high-latitude dwelling
355 mosasaurs compared to their low-latitude dwelling brethren. The Northwest Territories of
356 Canada are of particular interest, as only a mosasaur quadrate has been recovered from one
357 field site, located near the Anderson River, as a result of a single excavation (Russell,
358 1967). The quadrate bone (NMC 10429) was originally identified as *Platecarpus* but is now
359 identified as *Plioplatecarpus* (T. Konishi, personal communication, 2013). This
360 reidentification decreased the known distribution for *Platecarpus* to southern Manitoba
361 (paleolatitude of ~53°N) placing it with such smaller PF-bearing mosasaur genera as
362 *Tylosaurus* and *Clidastes*. Antarctica has also yielded the mosasaur genus
363 *Taniwhasaurus*—a close relative of *Tylosaurus*—from James Ross Island (~62°S) and Vega
364 Island (~60°S) (Fernández and Gasparini, 2012). Although *Tylosaurus*, itself, has yet to be

identified in Antarctica, two vertebrae (MLP 87-II-7-1) have been found on the nearby Seymour Island (~62°S) and are identified as tylosaurine (Fernández and Gasparini, 2012).

Other high-latitude mosasaur sites are more accessible but have mostly yielded fragments and partial remains of teeth and vertebrae. Western Australia, near Gingin, Dandaragan, and the Giralia Ranges, is a prime location as supposed remains of *Platecarpus* have been found in the Molecap Greensand (~58°S). These remains, however, lack a skull, are in poor condition, and have yet to be confidently identified (Kear et al., 2005). New Zealand sites have a similar paleolatitude (~58°S) and contain tylosaurine (Caldwell et al., 2005), mosasauridae (Wiffen, 1990), and other mosasaur specimens (Wiffen, 1990 and Consoli and Stilwell, 2009). Although mainly partial fragments have been identified—a single quadrate bone representing the *Mosasaurus* specimen (Wiffen, 1990)—two *Taniwhasaurus oweni* specimens (NMNZ R 1536 and KHM N99-1014) have been identified by their jugal, frontal, prefrontal, premaxilla, pterygoid, and even a PB (Caldwell et al., 2005). If more specimens of *Taniwhasaurus* with their PB intact are discovered in New Zealand and Antarctica, a new PF-analysis could be undertaken on this genus. This analysis would be particularly interesting as *Taniwhasaurus* has been constantly found in high-latitude field sites. The PF size of *Taniwhasaurus* could be compared to the PF size of its lower latitude cousin, *Tylosaurus*, via H1 in another PIC analysis. Japan (~42°N) has yielded mosasaurs relevant to this study, namely *Mosasaurus* (see Sato et al., 2012 for general occurrence of mosasaurs in Japan). The *Mosasaurus* specimens are represented mainly by teeth, vertebrae, and other skeletal fragments, but we are hopeful that more remains, especially their PB, will be extracted from the field sites. The Kristianstad Basin in Southern Sweden (~46°N) is another site in which partial

388 mosasaur remains of *Clidastes* (Lindgre and Siverson, 2004) and *Tylosaurus* (Lindgren and
389 Siverson, 2002), have been found. If enough viable specimens from these two genera were
390 recovered, we could observe if there is any difference in PF size between European and
391 North American specimens within the same genera.

392 Mosasaurs found in lower latitude sites could be used to retest H1 for within genera.
393 Mosasaurs have been identified, such as *Yaguarasaurus* and *Tethysaurus*, in Columbian
394 (~3°S) deposits (see Páramo-Fonseca, 2011 for a general review of their occurrences) and a
395 Columbian Campanian mosasaur (ING RC090805) has yet to be confidently identified as it
396 is currently under preparation (Bengtson and Lindgren, 2005). Two isolated *Platecarpus*
397 tooth-crowns have also been found in the Sergipe Basin in northeastern Brazil (~17°S)
398 (Bengtson and Lindgren, 2005). The Oulad Abdoun Basin in Morocco (~25°N) has also
399 produced an abundance of mosasaurs, as well as a recent number of publications identifying
400 and describing new mosasaurs (e.g., Bardet et al., 2004, 2005a, 2005b; Leblanc et al., 2012)
401 including specimens of *Mosasaurus*. Although no *Mosasaurus* specimens have yet been
402 found with intact PB, two *Eremiasaurus* specimens (UALVP 51744 and OCP DEK/GE
403 112) were both preserved with a nearly complete skull and vertebral column (Leblanc et al.,
404 2012).

405 Comprehensive studies of PE size (PF size and its skull position as proxies) in
406 extant lizard taxa with respect to their home range, latitude, altitude, and climate variables
407 would be useful to understand PF size variation in PE-bearing ancient animals. Only a few
408 studies (e.g., Gundy et al., 1975 and Labra et al., 2010) have intensely analyzed these
409 relationships so the amount of new information that could be obtained would greatly benefit
410 paleontological research. This could be accomplished by measuring PE, PF, and pineal

411 body size amongst different groups of closely related reptiles who live in vastly different
412 environments or latitudes such as *Liolaemus* (Labra et al., 2010). There could also be other
413 factors that affect PE size in modern reptiles that we are not aware of yet that could explain
414 why *Platecarpus* has a larger PE than *Clidastes* or *Tylosaurus.*

415 Lastly, we encourage further research on the relationship between the pineal body
416 and seasonal migration in migratory sea turtles for both low-latitude seas turtles—e.g., the
417 loggerhead sea turtle (*Caretta caretta*) and the green sea turtle (*Chelonia mydas*)—and such
418 high-latitude sea turtles as the leatherback sea turtle (*Dermochelys coriacea)*. The
419 methodology in the study of the leatherback sea turtle by Davenport et al. (2014) should be
420 followed to deduce the relationship between latitudinal distribution, water temperature, and
421 turtle movement throughout the year. If there is a relationship between migration and pineal
422 activity, this information could be applied to mosasaurs to test the new hypothesis proposed
423 here that the PE was used to trigger and control the latitudinal range of migration.
424

425 ## CONCLUSIONS

426 We tested two hypotheses for this study concerning the PF of mosasaurs (Table 1).
427 We found that there is a weak but nonsignificant relationship between PF size and
428 paleolatitudinal distribution among mosasaur genera. *Plioplatecarpus* has both the largest
429 PF and the highest known distribution of mosasaurs. The mosasaur with the second largest
430 PF, *Platecarpus*, however, shared a similar paleolatitudinal extent with other, much smaller
431 PF-bearing mosasaurs, such as *Clidastes*, *Mosasaurus*, and *Tylosaurus*. There was also a
432 nonsignificant relationship between PF size and paleolatitude distribution within mosasaur
433 genera. We also determined that there was no relationship between the presence of

avascular necrosis and PF size. As such, we reject both hypotheses. We propose a new hypothesis that the PE (PF as the proxy) was used for migrational behaviors, as the PE could be a used as a trigger for seasonal migration due to changes in day length and incident angle of sunlight. The substantial difference in PF sizes among *Platecarpus* and other mosasaur genera ($p<0.001$ in Fisher's LSD test) warrants future investigation into why *Platecarpus* evolved a large PE. This study can be used as a framework to test the function of the PE, with the PF as a proxy, in other extinct vertebrates, such as the marine plesiosaurs (Lepidosauromorpha) and the terrestrial therapsids (Synapsida).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Appendix 1: Relative parietal foramen size in lizards as arranged by species. Relative size as determined by area of the parietal foramen to the area of the occipital condyle (OC)

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| Catalogue Number | Species Name | Location Found | Degrees | Area of PF (mm2) | Area of OC (mm2) | PF/OC |
|---|---|---|---|---|---|---|
| 93452 | *Basiliscus basiliscus* | WED 19022, Neotropical / Central America Costa Rica Puntarenas : 6 km SE Palmar Sur | 10 | 0.248 | 9.191 | 0.027 |
| 93453 | *Basiliscus basiliscus* | WED 19023, Neotropical / Central America Costa Rica Puntarenas : 6 km SE Palmar Sur | 10 | 0.505 | 5.762 | 0.088 |
| 93454 | *Basiliscus basiliscus* | WED 19024, Neotropical / Central America Costa Rica Puntarenas : 6 km SE Palmar Sur | 10 | 0.31 | 5.889 | 0.053 |
| 16423 | *Crotaphytus collaris* | NA, Nearctic USA Kansas Greenwood: No locality data | 38 | 1.971 | 1.836 | 1.074 |
| 16431 | *Crotaphytus collaris* | NA, Nearctic USA Kansas Greenwood: No locality data | 38 | 1.599 | 1.549 | 1.032 |
| 21003 | *Crotaphytus collaris* | NA, Nearctic USA Kansas Meade: 1 mi W State Lake | 37 | 0.26 | 2.535 | 0.103 |
| 157875 | *Crotaphytus reticulatus* | RRM 1691, Nearctic USA Texas Maverick: 1 mi E Eagle Pass, Manges Ranch | 29 | 0.289 | 3.761 | 0.077 |
| 157876 | *Crotaphytus reticulatus* | RRM 1693, Nearctic USA Texas Maverick: 1 mi E Eagle Pass, Manges Ranch | 29 | 0.427 | 3.678 | 0.116 |
| 147266 | *Crotaphytus reticulatus* | Texas: Maverick Co. | 29 | 0.369 | 1.928 | 0.191 |
| 121764 | *Gambelia silus* | California: Fesno Co: Little Panoche RCH | 36 | 0.598 | 3.59 | 0.167 |
| 121749 | *Gambelia silus* | California: Fresno Co: Little Panoche RCH | 36 | 0.733 | 3.575 | 0.205 |
| 121757 | *Gambelia silus* | California: Fresno Co: Little Panoche RCH | 36 | 1.562 | 3.795 | 0.412 |
| 84971 | *Ctenosaura similis* | LMH 2046, Neotropical / Central America Nicaragua Managua : 2 km N Sabana Grande | 12 | 0.488 | 5.754 | 0.085 |
| 84957 | *Ctenosaura similis* | Nicaragua: Chinandega: 4km N, 2 km W Chichigalpa | 13 | 0.117 | 7.124 | 0.016 |
| 19602 | *Ctenosaura similis* | Yucatan Peninsula: Cozume Island | 20 | 0.408 | 12.063 | 0.034 |
| 160897 | *Diplolaemus darwini* | WED 44738, Neotropical / South America Argentina Neuquen : S shore Laguna Blanca | 39 | 1.397 | 3.305 | 0.423 |
| 121765 | *Gambelia silus* | California: Fresno Co: Merch Hot Spr. | 36 | 1.009 | 3.306 | 0.305 |
| 121774 | *Gambelia silus* | California: Fresno Co: Wasco | 36 | 1.046 | 3.889 | 0.269 |
| 21000 | *Holbrookia maculata* | NA, Nearctic USA Kansas Clark: Stephenson Ranch | 37 | 1.205 | 0.795 | 1.516 |
| 20997 | *Holbrookia maculata* | NA, Nearctic USA Kansas Meade: 1 mi W State Lake | 37 | 0.11 | 1.105 | 0.100 |
| 1893 | *Holbrookia maculata* | NA, Nearctic USA Kansas Stafford: Big Salt Marsh | 38 | 0.394 | 1.454 | 0.271 |
| 29984 | *Iguana iguana* | Mexico: Veracruz: Boca del rio | 19 | 10.171 | 49.996 | 0.203 |
| 84974 | *Iguana iguana* | CJC 925, Neotropical / Central America Nicaragua Chinandega : 4 km N, 2 km W | 13 | 1.148 | 20.009 | 0.057 |
| 84979 | *Iguana iguana* | LMH 2674, Neotropical / Central America Nicaragua Rivas : Rio Javillo; 3 km N, 4 km W | 11 | 1.725 | 21.827 | 0.079 |
| 161108 | *Liolaemus elongatus* | WED 44656, Neotropical / South America Argentina Neuquen : S shore Laguna Blanca | 39 | 0.392 | 1.488 | 0.263 |
| 161109 | *Liolaemus elongatus* | WED 44657, Neotropical / South America Argentina Neuquen : S shore Laguna Blanca | 39 | 0.68 | 1.706 | 0.399 |

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|---|---|---|---|---|---|---|
| 7230 | *Phrynosoma coronatum* | RHS 136, Nearctic USA California Los Angeles: Los Angeles | 34 | 1.89 | 4.19 | 0.451 |
| 7231 | *Phrynosoma coronatum* | RHS 137, Nearctic USA California Los Angeles: Los Angeles | 34 | 1.39 | 3.766 | 0.369 |
| 13950 | *Sceloporus clarki* | JEH 139, Nearctic USA New Mexico Catron: 5 mi N Glenwood | 34 | 1.999 | 3.775 | 0.530 |
| 13955 | *Sceloporus clarki* | WKM 6, Nearctic USA Arizona Maricopa: 30 mi SW Phoenix | 33 | 1.905 | 3.438 | 0.554 |
| 13956 | *Sceloporus clarki* | CWH 6, Nearctic USA New Mexico Catron: No locality data | 34 | 0.988 | 3.083 | 0.320 |
| 13964 | *Sceloporus jarrovii* | CWH 49, Nearctic USA Arizona Santa Cruz: No locality data | 32 | 1.759 | 1.667 | 1.055 |
| 13965 | *Sceloporus jarrovii* | CWH 45, Nearctic USA Arizona Santa Cruz: No locality data | 32 | 3.062 | 1.836 | 1.668 |
| 117458 | *Sceloporus malachiticus* | JDL 479, Neotropical / Central America Costa Rica San Jose : Cerro de la Muerte | 10 | 1.958 | 1.7 | 1.152 |
| 117459 | *Sceloporus malachiticus* | JDL 480, Neotropical / Central America Costa Rica San Jose : Cerro de la Muerte | 10 | 2.554 | 1.538 | 1.661 |
| 117460 | *Sceloporus malachiticus* | JDL 481, Neotropical / Central America Costa Rica San Jose : Cerro de la Muerte | 10 | 1.772 | 1.733 | 1.023 |
| 147319 | *Stenocercus guentheri* | Ecuador: Cotopaxi: Mulalo | 1 | 0.124 | 2.221 | 0.056 |
| 147326 | *Stenocercus guentheri* | Ecuador: Cotopaxi: Mulalo | 1 | 0.107 | 1.379 | 0.078 |
| 134089 | *Stenocercus nigromaculatus* | Peru: Piura: Huancabamba | 5 | 0.071 | 0.996 | 0.071 |
| 134092 | *Stenocercus nigromaculatus* | Peru: Piura: Huancabamba | 5 | 0.105 | 1.443 | 0.073 |
| 133878 | *Stenocercus ochoai* | Peru: Cusco: 10km N Ollantaytambo | 13 | 0.069 | 1.445 | 0.048 |
| 133884 | *Stenocercus ochoai* | Peru: Cusco: 10km N Ollantaytambo | 13 | 0 | N/A | 0 |
| 134198 | *Stenocercus variabilis* | Peru: Ayacucho | 13 | 0 | N/A | 0 |
| 134213 | *Stenocercus variabilis* | Peru: Ayacucho | 13 | 0 | N/A | 0 |
| 142704 | *Stenocercus varius* | Ecuador: Pichincha; Fincha Santa Lucia | 0 | 0 | N/A | 0 |
| 121135 | *Stenocercus varius* | Ecuador: Pichincha: Tandapi | 0 | 0 | N/A | 0 |
| 134563 | *Stenocercus varius* | Ecuador: Pichincha: Tandapi | 0 | 0 | N/A | 0 |
| 167513 | *Tropidurus Cf.* | Venezuela: Bolivar | 10 | 0.077 | 1.571 | 0.049 |
| 165708 | *Tropidurus Cf. Hispidus* | Venezuela: Bolivar | 10 | 0.038 | 3.749 | 0.010 |
| 135268 | *Tropidurus hispidus* | MLC 2101, Neotropical / South America Brasil Para : IPEAN, 3 km E Belem | 6 | 0.084 | 3.939 | 0.021 |
| 135269 | *Uranoscodon superciliosus* | MLC 2139, Neotropical / South America Brasil Para : IPEAN, 3 km E Belem | 6 | 1.519 | 4.425 | 0.343 |
| 128215 | *Uranoscodon superciliosus* | MLC 1546, Neotropical / South America Brasil Para : IPEAN, 3 km E Belem | 6 | 1.657 | 4.237 | 0.391 |
| 29255 | *Urosaurus bicarinatus* | Mexico; Jalisco; 5 mi. W Chapala | 20 | 0.278 | 1.067 | 0.261 |
| 61524 | *Urosaurus bicarinatus* | Guerrero; Agua del Obispo | 18 | 0.146 | 0.661 | 0.221 |